Observations on the Oxygen Consumption of Certain Marine Crustacea[1]

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MANY PAPERS dealing with the respiration of Crustacea with respect to ecological problems have appeared (Bull, 1931; Edwards and Irving, 1943; van Heerdt, 1940; van Heerdt and Krijgsman, 1939; Hyman, 1932; Johnson, 1936; Munro Fox and Simmonds, 1933; Munro Fox and Johnson, 1933, 1934; Peters, 1935; Raffy, 1934; Thienemann, 1928), but a number of these seem to give results of dubious validity. The oxygen consumption has been measured under different conditions of temperature, oxygen tension, etc. More recently the effect of carbon dioxide on the oxygen consumption has also been studied (Johnson, 1936; van Heerdt, 1940; van Heerdt and Krijgsman, 1939; Schlieper and Peters, 1937; Segaar, 1941). However, comparative studies using the same method and technique on a number of Crustacea from different habitats are rare, although the results of such investigations would have a positive bearing on ecological and comparative physiological problems. It is well known that many animals, living in a special habitat, may show a distinct physiological adaptation to that habitat. Therefore, the oxygen consumption, at varying oxygen tensions, was studied in a number of Crustacea from different and specific habitats.

MATERIALS AND METHOD

The following species were selected: *Metopograpsus messor* Forskål, a crab which apparently lives for the most part out of the water; *Pseudozius caystrus* Adams and White, which lives underneath rocks in the tidal zone; *Phymodius ungulatus* Milne Edwards and *Platypodia granulosa* Rüppell, which are found in abundance between branches of coral; *Pseudosquilla ciliata* Miers and *Calappa hepatica* Linn., which live on and in sandy flats rather devoid of organic matter (as compared with muddy flats); *Podophthalmus vigil* Fabricius, a swimming crab found in large numbers on and in muddy flats rich in organic matter.

To determine the oxygen consumption at different tensions, each animal was placed in a glass tube 20 centimeters long and with an inner diameter of 26 millimeters. This tube was closed with rubber stoppers through which were inserted a glass inlet tube at one end, and an outlet tube and a thermometer at the other end. Water, containing a known quantity of oxygen in solution, flowed from a carboy through the tubes. An overflow, which gave a constant head of pressure, and screw clamps adjusted the flow and kept it at a constant rate of 50 cubic centimeters per minute (3 liters per hour). Care was taken that no air bubbles remained in the whole system. Samples of 125 cubic centimeters were taken from the in- and outflowing water (5 minutes "overflow time" was allowed to prevent errors caused by absorption of oxygen from the air) and immediately titrated (Winkler method) to determine the quantity of oxygen present. The animals were left in the flowing water for at least 30 minutes before a sample was taken, whenever water of different oxygen content was used. Control experiments showed that this period of time

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was sufficient to equilibrate the oxygen consumption in the new medium. This method also precluded the possibility of an accumulation of excretions which might affect the results of the Winkler titration.

The animals could move in their containers, but usually they very soon became inactive and quiet. However, inasmuch as they were not artificially immobilized and did move now and then, certain fluctuations did appear in the oxygen consumption. This condition was included because it is known (Jordan and Guittart, 1938) that artificial immobilization markedly affects the rate of oxygen consumption. The results of experiments with animals, which for some reason or other remained restless, were discarded because their oxygen consumption was very irregular, as could be expected.

The percentage of oxygen in the water in the carboy was varied by bubbling nitrogen through it for varying periods of time or by adding normal sea water to oxygen-deficient water. As the present investigation was concerned with the effect of varying oxygen tensions on the oxygen consumption at normal temperatures and as no method of maintaining the temperature at a constant room temperature was available, no special provisions were made to keep the temperature at a constant level throughout all experiments. However, the large carboys (5-gallon capacity) insured a comparatively constant temperature during a whole experiment, the greatest difference encountered being 0.5°C. between start and finish.

Several attempts were made to count the number of beats per minute of the scaphognathites and pleopods. At the normal high temperature their movements were so quick and the rhythm often so irregular (especially at lower oxygen tensions) that it was impossible to obtain satisfactory counts. However, it was sometimes possible to observe an increase or decrease of the rate of the beats.

Prior to each experiment the animals were starved for 24 hours.

EXPERIMENTS

The results of the determinations of the oxygen content of in- and outflowing water are presented in Table 1, which also includes the weight of each animal and the temperature of the water. The percentage of oxygen consumed by the animals as a function of oxygen present in the inflowing water has been computed.

TABLE 1

THE PERCENTAGE OF OXYGEN CONSUMED FROM FLOWING WATER OF VARIED OXYGEN CONCENTRATION BY SEVERAL SPECIES OF CRUSTACEA

SPECIES	CC. OF O_2 PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
Pseudozius caystrus	6.24	6.08	2.6
Weight	6.24	6.06	2.9
3 grams	6.09	5.93	2.6
Temperature	5.28	5.18	1.9
27.5–27.8°C.	4.38	4.26	2.7
	4.38	4.23	3.4
	4.38	4.20	4.1
	2.88	2.83	1.7
	2.88	2.84	1.4
	2.59	2.42	6.6
	2.17	1.99	8.3
	1.67	1.57	6.0
	1.67	1.57	6.0
	1.27	1.18	7.1
	1.27	1.14	10.2
	1.21	1.11	8.3
	1.18	1.13	4.2
	1.18	1.13	4.2
Weight	6.18	6.01	2.8
2.9 grams	6.12	5.97	2.5
Temperature	6.12	5.98	2.6
26.6–27.0°C.	5.61	5.50	2.3
	4.40	4.31	2.1
	4.40	4.29	2.5
	3.83	3.76	1.9
	3.51	3.46	1.4
	2.90	2.86	1.4
	2.63	2.48	5.7
	2.08	1.93	7.0
	1.80	1.66	7.8
	1.59	1.46	8.2
	1.31	1.19	9.1
	1.31	1.20	8.5
	1.12	1.08	3.6
	1.12	1.07	4.5
	1.12	1.07	4.5

TABLE 1 (Continued)

SPECIES	CC. OF O_2 PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
Metopograpsus messor	6.24	6.03	3.4
Weight	6.24	6.08	2.6
5.9 grams	5.71	5.62	1.6
Temperature	5.71	5.64	1.2
27.5–27.8°C.	5.28	5.16	2.3
	5.28	5.19	1.7
	4.38	4.18	4.5
	4.38	4.21	3.9
	3.91	3.79	3.1
	3.91	3.82	2.3
	2.88	2.81	2.4
	2.88	2.78	3.4
	2.59	2.40	7.3
	2.59	2.45	5.4
	2.17	1.93	11.1
	2.17	1.98	8.8
	1.27	1.10	13.4
	1.27	1.09	15.7
	1.21	1.07	11.6
	1.21	1.09	9.9
	1.18	1.06	10.2
	1.18	1.07	9.3
	0.96	0.93	3.1
Weight	6.18	6.01	2.8
6.2 grams	6.12	5.97	2.5
Temperature	6.12	5.94	2.9
26.6–27.0°C.	5.61	5.50	2.0
	4.40	4.29	2.5
	4.40	4.25	3.4
	3.83	3.70	3.4
	3.51	3.40	3.1
	2.90	2.81	2.8
	2.63	2.57	2.3
	2.08	1.92	7.7
	1.80	1.60	11.1
	1.59	1.40	12.0
	1.31	1.16	11.4
	1.31	1.16	11.4
	1.12	1.03	8.0
	1.12	1.05	6.3
	1.12	1.06	5.4
Calappa hepatica	4.19	3.57	14.8
Weight	4.19	3.57	14.8
7.9 grams	4.17	3.64	12.7
Temperature	4.17	3.49	16.3
26.0–26.2°C.	4.15	3.80	8.4
	4.14	3.73	9.9
	4.14	3.73	9.9
	4.14	3.71	10.4
	4.09	3.73	8.8
	3.68	3.24	12.0
	3.68	3.16	14.0
	3.49	3.10	11.3
	3.39	2.87	15.3

TABLE 1 (Continued)

SPECIES	CC. OF O_2 PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
	3.30	2.81	14.8
	3.28	2.73	16.8
	3.18	2.80	12.0
	2.99	2.52	15.7
	2.75	2.33	15.3
	2.69	2.33	13.4
	2.61	2.19	16.1
	2.58	2.24	13.2
	2.20	1.76	20.1
	1.98	1.55	21.7
	1.83	1.37	25.1
	1.59	1.22	23.3
	1.54	1.19	22.7
	1.45	1.05	27.6
	1.35	0.98	27.4
	1.31	1.01	22.9
	1.19	1.00	16.0
Weight	4.23	3.64	13.9
6.8 grams	4.23	3.68	13.0
Temperature	4.10	3.48	15.1
26.1–26.4°C.	4.08	3.48	14.7
	3.53	3.11	11.9
	3.20	2.84	11.3
	2.61	2.15	17.6
	2.20	1.78	19.1
	2.18	1.73	20.6
	2.18	1.72	21.1
	1.91	1.47	22.0
	1.80	1.37	23.9
	1.80	1.36	24.4
	1.37	1.03	24.9
	1.37	1.05	23.4
	1.37	1.03	24.9
	1.14	0.98	14.0
Pseudosquilla ciliata	4.19	3.86	7.9
Weight	4.19	3.86	7.9
4.7 grams	4.17	3.87	7.2
Temperature	4.15	4.02	3.1
26.0–26.2°C.	4.14	3.95	4.6
	4.14	4.05	2.2
	4.14	4.07	1.7
	4.09	3.85	5.9
	3.68	3.56	3.3
	3.50	3.33	5.0
	3.28	3.22	2.4
	2.99	2.89	3.3
	2.75	2.64	4.0
	2.74	2.57	6.2
	2.73	2.61	4.4
	2.69	2.53	5.9
	2.61	2.48	3.1
	2.58	2.42	5.9
	2.20	1.97	10.3
	2.00	1.77	11.5

TABLE 1 (Continued)

SPECIES	CC. OF O_2 PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
	1.98	1.71	13.9
	1.59	1.36	14.5
	1.45	1.27	12.4
	1.31	1.15	12.2
Phymodius ungulatus	4.53	3.75	17.2
Weight	4.53	3.89	14.1
12.5 grams	3.46	3.12	9.8
Temperature	3.12	2.90	7.1
26.8°C.	2.98	2.86	4.0
	2.93	2.59	11.6
	2.93	2.55	13.0
	2.66	2.33	12.4
	2.46	2.03	17.5
	2.35	1.78	24.3
	1.78	1.28	28.1
	1.50	1.30	13.3
	1.34	1.16	13.4
Weight	4.56	3.92	14.0
11.9 grams	4.41	3.77	14.5
Temperature	3.59	3.23	10.0
26.5–26.8°C.	3.59	3.26	9.2
	2.92	2.51	14.0
	2.71	2.35	13.3
	2.60	2.26	13.0
	2.38	1.92	19.3
	2.33	1.85	20.6
	1.85	1.52	17.8
	1.61	1.38	14.3
	1.61	1.39	13.7
	1.28	1.11	13.3
Platypodia granulosa	4.53	3.57	21.2
Weight	4.53	3.42	24.5
6.0 grams	3.46	2.88	16.8
Temperature	3.12	2.58	17.3
26.8°C.	2.98	2.57	13.8
	2.93	2.40	18.1
	2.93	2.53	13.7
	2.66	2.14	19.5
	2.53	2.18	13.8
	2.46	2.05	16.7
	2.35	1.72	26.8
	1.78	1.35	24.2
	1.50	1.14	24.0
	1.34	0.98	26.9
Weight	4.56	3.48	23.7
6.3 grams	4.41	3.49	20.9
Temperature	3.59	2.97	17.3
26.5–26.8°C.	2.92	2.41	17.5
	2.71	2.25	17.0
	2.60	2.18	16.2
	2.33	1.70	27.0
	2.33	1.71	26.6

TABLE 1 (Continued)

SPECIES	CC. OF O_2 PER LITER		PERCENTAGE OF OXYGEN CONSUMED
	Inflow	Outflow	
	1.85	1.41	23.8
	1.85	1.41	23.8
	1.61	1.22	24.2
	1.61	1.22	24.2
	1.28	1.00	21.9
	1.28	1.00	21.9
Podophthalmus vigil	4.02	3.68	8.5
Weight	3.93	3.59	8.7
10.0 grams	3.16	2.73	13.6
Temperature	3.02	2.59	14.1
26.5–26.8°C.	2.95	2.56	13.2
	2.63	2.29	12.9
	2.48	2.16	12.9
	2.33	1.96	15.5
	2.13	1.87	12.2
	1.99	1.67	16.1
	1.79	1.53	14.5
	1.60	1.36	15.0
	1.41	1.19	15.6
	1.38	1.10	20.3
	1.34	0.98	26.9
Weight	4.53	4.19	7.5
11.1 grams	4.11	3.76	8.5
Temperature	3.78	3.41	9.8
26.3–26.6°C.	3.09	2.68	13.3
	3.00	2.64	12.0
	2.73	2.36	13.6
	2.38	2.08	12.6
	2.25	1.97	12.0
	2.01	1.74	13.4
	1.85	1.57	15.0
	1.75	1.50	14.3
	1.54	1.31	14.9
	1.43	1.40	16.1
	1.32	0.99	25.0
	1.20	0.97	19.1
	1.17	0.98	16.2

DISCUSSION AND CONCLUSIONS

With respect to adaptation in the consumption of oxygen, two main groups of animals can be distinguished: (1) those animals which show a *regulation* and (2) those showing an *adjustment*. The first group possesses mechanisms which permit the consumption of constant quantities of oxygen per unit of time, even when the oxygen tension varies markedly. They therefore actively regulate their respiration. The second group is unable to

do so. Consequently, their oxygen consumption varies (more or less) proportionately with the oxygen tension of the surroundings.

The Crustacea used in these experiments obviously belong to the large group of animals with an adjustable respiration. They lack the ability to regulate (at least to any appreciable extent) their oxygen consumption when the oxygen content of the water is altered. The oxygen consumption varies with the oxygen tension (Maloeuf, 1936) and according to Amberson *et al.* (1924) may even be directly proportional to it. Our experiments confirm this (Table 1). *Phymodius ungulatus* and *Platypodia granulosa* seem to consume even less oxygen than expected when the oxygen content of the water is first reduced. After this initial period, however, oxygen consumption proportionate to the tension becomes apparent.

It has been claimed that many Crustacea do have a regulating mechanism in that they increase the rhythm of the beat of the scaphognathites and pleopods when the oxygen content of the water decreases (Munro Fox *et al.*, 1933, 1934; Johnson, 1936; Schlieper and Peters, 1937; van Heerdt and Krijgsman, 1939; van Heerdt, 1940). As these structures are the propellers by means of which the water flow is directed over the gills, an increase of the beat will bring the gills in contact with a larger quantity of water from which, consequently, more oxygen can be absorbed. In such cases some kind of regulation may be expected, not a typical adjustment as found in our experiments. Although, as mentioned before, we have been unable to make exact counts, in some cases an increase in the beat was noted when the oxygen tension of the water started to decrease. This would therefore point toward a regulation; but if so, then it must be very weak and is therefore not apparent in the direct results. However, when the utilization of oxygen (the oxygen consumed expressed as the percentage of the available oxygen in the water) is studied, such a weak regulation may eventually be found. As long as the utilization remains constant when the oxygen tension of the water decreases, it means that there is little or no regulation, and the respiration is therefore of the adjustable type. When the utilization curve rises, it means that there is some regulation, that more oxygen is consumed than would be the case in the adjustment type of respiration. A drop of the curve means a decrease in oxygen consumption, as compared with the adjustment type of respiration.

Before the results with respect to the utilization of oxygen can be discussed, the question arises as to what can be the (primary) cause of regulation or adjustment in the process of respiration. Considering the simplest possibility, this is based on a limiting factor. Respiration being *de facto* an oxidation, the limiting factor can be either the oxidizable substances or the oxygen available. If there is an ample quantity of the former, the amount of oxygen reaching these substances must be regulated to maintain oxidation at a constant level. To increase (or decrease) this level, more (or less) oxygen must be admitted. Here oxygen is clearly the limiting factor. In the case of the oxidizable substances being the limiting factor, the rate of oxidation is determined by the amount of such substances made available by the organism.

An objection may be raised in that the possibility might exist that there is a complete tissue oxygen saturation in the organism which becomes unsaturated at lower tensions, resulting in increased utilization at that point. In that case, however, the utilization curve will steadily rise with decreasing oxygen tension of the water, because the quantity of oxygen consumed by the tissues remains constant. This is not the case (Figs. 1–7). Admittedly, the alternative between "fuel" (oxidizable substances) and available oxygen as limiting factors is probably too simple but is unavoidable at this time as far too little is known of the intracellular respiration processes in Crustacea to include them in the picture. As long as such processes in this

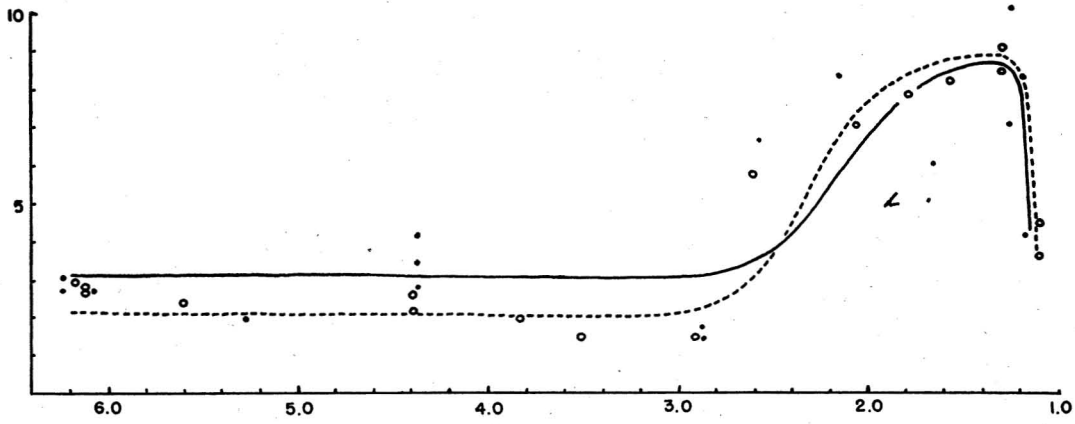

FIG. 1. Oxygen utilization in *Pseudozius caystrus*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

group of animals are not well understood, a simple picture seems preferable and justified.

According to our results (Table 1), the amount of oxygen consumed decreased with the decrease of the oxygen present over the entire range of the experiments. Oxygen seems, therefore, to be the limiting factor. If so, the utilization curve must run parallel to the abscissa. But this is not the case for the entire curve. Figures 1–4 show, for example, that as soon as the oxygen content of the water reaches a certain low level (*Pseudozius* 2.8–3 cc. O_2/l., *Metopograpsus* 2.8–3.2 cc. O_2/l., *Calappa* 3.0–3.2 cc. O_2/l., and *Pseudosquilla* about 2.9 cc. O_2/l.) the utilization curve rises. This points definitely toward a regulation,

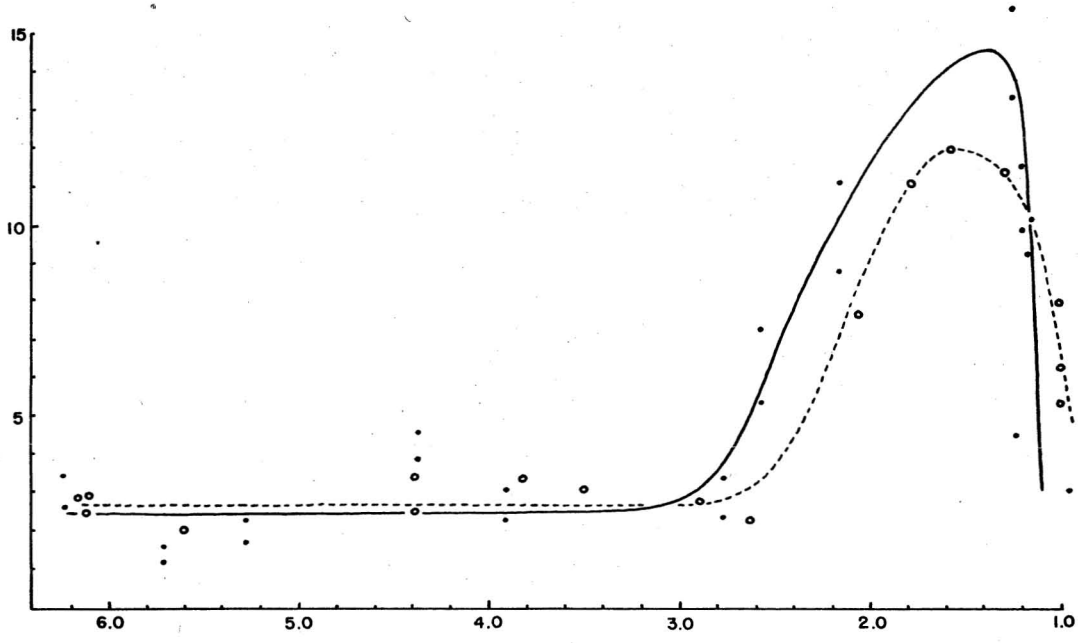

FIG. 2. Oxygen utilization in *Metopograpsus messor*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

which is probably not the result of a sudden increase of the rhythm of the beat of the scaphognathites or pleopods, because such a sudden increase was never observed. On the contrary, at low oxygen tensions these structures very often beat quite irregularly, but apparently more slowly. This means, therefore, that oxygen is no longer the limiting factor in oxygen consumption. The fact that the amount of available oxygen decreases whereas its utilization increases and the water propelling mechanisms do not show a sudden acceleration can have but one meaning: more oxidizable substances become available for (direct) oxidation. This must be the result

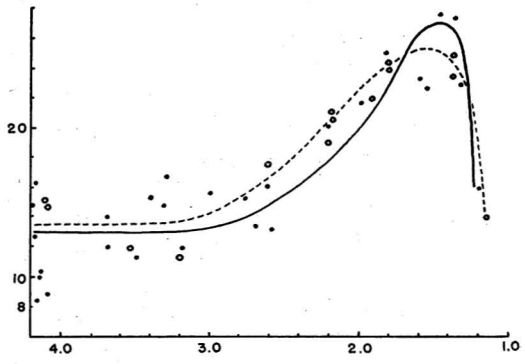

FIG. 3. Oxygen utilization in *Calappa hepatica*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

of a change in metabolic processes which produce such readily oxidizable substances. Such a metabolic mechanism must be considered an important "safety measure" to the animals, as they can now maintain life under conditions which would probably prove fatal without it. However, it does not actually change the animal from an "adjustment" into a "regulation" type, as the total oxygen consumption continues decreasing with the oxygen content of the water. A moment will come at which the amount of oxidizable substances set free in the tissues is no longer sufficient to maintain life with the available oxygen. Then the utilization curve will de-

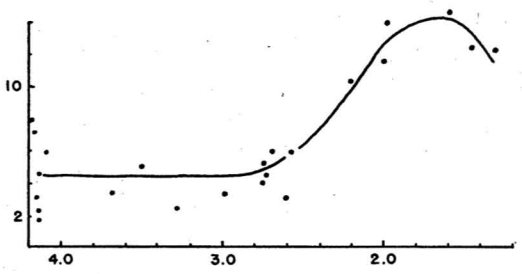

FIG. 4. Oxygen utilization in *Pseudosquilla ciliata*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

crease sharply (Figs. 1–7), and death will be the result in a comparatively short time. At the relatively high temperatures encountered in Hawaii, the crabs usually die in 1 to 2 hours when the water contains less than 0.96 cc. O_2/l., but they stay alive for at least 3 hours when 1.4 cc. O_2/l. is present. At lower temperatures, wherein the metabolism is at a much lower level, they seem to withstand lower oxygen tensions successfully. Jordan and Guittart (1938) reported, for instance, that at 13°C. *Potamobius fluviatilis* lived for 2.5 hours in water containing only 0.35 cc. O_2/l., after which period the experiment was terminated.

The suggestion that certain substances used in respiration are liberated by the tissues, by

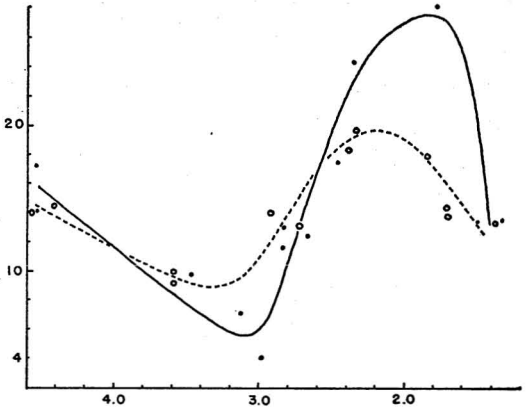

FIG. 5. Oxygen utilization in *Phymodius ungulatus*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

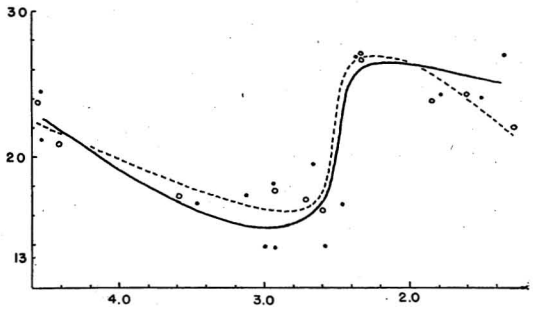

FIG. 6. Oxygen utilization in *Platypodia granulosa*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

some life process, at low oxygen tensions is not as hypothetical as it seems to be. Helff (1928) has already discussed the possibility of oxygen being secreted by the tissues, but this idea has been rejected, chiefly because of errors in his experimental method (Maloeuf, 1936). Recently Harnisch (1951), using a better technique, reached the same conclusion in his experiments on *Chironomus* larvae. He was able to prove this assumption correct by investigating the hemoglobin of the larvae spectrophotometrically: at very low oxygen tensions the hemoglobin contained more oxygen than would be possible without such a secretion. By observing the living animal continuously, he could actually observe the re-oxidation of the reduced hemoglobin. When, however, the oxygen reserve was consumed (probably because of a weakening of the life processes necessary to liberate the oxygen, which means that the latter was not present in reserve as free oxygen), re-oxidation of the hemoglobin ceased. Koenen (1951) also mentioned the sudden rise of oxygen consumption at low oxygen tensions in her experiments.

The utilization curves of *Phymodius* and *Platypodia* (Figs. 5, 6) slope down in the beginning of the experiment. This may be caused by an ineffective propelling mechanism. At 3–3.2 cc. O_2/l. (*Phymodius*) and 2.9–3.1 cc. O_2/l. (*Platypodia*), we again get the sudden rise of the curve, followed by the now familiar decrease at 1.8–2.2 cc. O_2/l.

The mud-dweller *Podophthalmus*, on the other hand, shows from the beginning a slight increase of the utilization curve (Fig. 7) which may be due to a more effective stroke of the scaphognathites. Some regulation might be expected in an animal living in a habitat that is usually poor in oxygen. Because of the adaptation to such a habitat, we would also expect the safety measure to occur at a lower oxygen tension than in animals normally living in much better aerated water. The curve shows, indeed, a steep rise at 1.5 cc. O_2/l. The final drop seems to occur at around 1.3 cc. O_2/l. How do these data fit into the ecological pattern? We cannot expect the safety measure to be thrown into gear at very low oxygen tensions in *Metopograpsus* (practically an air-breather), *Pseudozius* (which lives in well-aerated water of the tidal zone), or *Phymodius* and *Platypodia* (which live on corals). Here, due to currents and, during the day, to photosynthesis by algae, the water is certainly not poor in oxygen. *Calappa* and *Pseudosquilla*, living on sandy flats in shallow water, seem to be in a less favorable situation. However, the organic matter present is not very abundant (as compared with organic mud), and minute algae covering the surface will produce during the day a fairly abundant

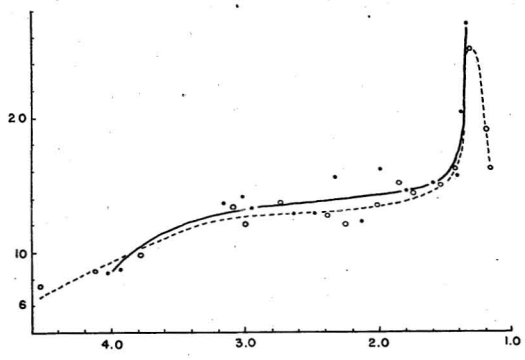

FIG. 7. Oxygen utilization in *Podophthalmus vigil*. Abscissa—cubic centimeters of oxygen per liter of water; ordinate—percentage of oxygen consumed from the oxygen available.

supply of oxygen, so that only during the night an appreciable drop of the oxygen tension of the water may be expected. Again, currents and tides will counteract this drop in part, so that the local oxygen deficiency is probably not very great.

With *Podophthalmus* the picture is a different one. The crab, which swims surprisingly little and remains buried in the mud during the day, lives in a habitat decidedly poor in oxygen. A physiological adaptation could be expected and is apparent: utilization shows a gradual but definite increase until a level of 3 cc. O_2/l. is reached, after which it increases more slowly and evenly until the water contains 1.4 cc. O_2/l., at which point the safety measure is thrown into gear.

SUMMARY

1. The oxygen consumption of *Metopograpsus messor* Forskål, *Pseudozius caystrus* Adam and White, *Phymodius ungulatus* Milné Edwards, *Platypodia granulosa* Rüppell, *Calappa hepatica* Linn., *Pseudosquilla ciliata* Miers, and *Podophthalmus vigil* Fabricius in running sea water of varying oxygen tensions was studied. All these animals belong to the so-called adjustable type of respirers, in that oxygen consumption decreases more or less proportionately with the oxygen tension of the water.

2. Analysis of the utilization of oxygen (percentage of oxygen consumed from the available oxygen) shows that at low oxygen tensions the metabolism of the animals changes, a change which counteracts partly the lack of oxygen of the surroundings.

3. The ecological importance of the different types of oxygen utilization is discussed.

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